Taxonomic notes on hummingbirds (Aves: Trochilidae). 1. Eriocnemis dyselius Elliot, 1872 is a melanistic specimen of Eriocnemis cupreoventris (Fraser, 1840)

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Abstract.—Eriocnemis dyselius Elliot, 1872 is hypothesized to be a melanistic specimen of Eriocnemis cupreoventris (Fraser, 1840), a puffleg hummingbird restricted to the Andes Mountains of Colombia and Venezuela.

Among the families of birds, the systematics of the Trochilidae are the most confused, in absolute numbers, by hybrids, genetic variants, and the problems associated with taxa described from unique specimens (e.g., Berlioz & Jouanin 1944; Banks & Johnson 1961; Greenway 1978; Bleiweiss 1988; Graves 1990, 1993, 1996, 1997a, 1997b; Hinkelmann et al. 1991). One such questionable taxon is Eriocnemis dyselius Elliot, 1872 a puffleg hummingbird of indeterminate origin. Salvin (1892:369) suggested that the black-plumaged specimen was "perhaps a melanism of E. cupreiventris," an inhabitant of forest borders and shrubby slopes (1950-3000 m) of the Venezuelan Andes and the Eastern Cordillera of the Colombian Andes (Hilty & Brown 1986, Fieldså & Krabbe 1990). Salvin did not elaborate on this proposal. Subsequent authors (Cory 1918, Berlioz & Jouanin 1944, Peters 1945, Greenway 1978, Fjeldså & Krabbe 1990) agreed with Salvin but likewise provided no further support for this hypothesis. Consequently, the taxonomy of E. dyselius is still uncertain. Here I present evidence that supports Salvin's (1892) conjecture that the holotype of E. dyselius is a melanistic specimen of Eriocnemis cupreoventris (Fraser, 1840).

Materials and Methods

The unsexed holotype of *Eriocnemis dy*selius (Fig. 1), a partially relaxed taxidermy mount with glass eyes, is adult as judged by the lack of striations on the maxillary ramphothecum (see Ortiz-Crespo 1972). Previously housed in both the Bourcier and Elliot collections (see Greenway 1978), the specimen is now catalogued in the American Museum of Natural History (AMNH 38452). I studied the specimen taking the approach outlined in Graves (1990) and Graves & Zusi (1990). In determining the scope of the species pool to be investigated, Elliot's (1872: 294) description offers little guidance:

"Four specimens, precisely alike, were, as I was informed, contained in the small collection of birds from which my example was taken; and, although no locality was given, it is supposed that Ecuador is the habitat of the species."

The existence of four similar specimens of unknown origin should not be interpreted as evidence of a differentiated population. Millinery dealers in the 19th century sorted and high-graded shipments of hummingbird skins for unusual specimens to offer to collectors of natural history specimens. Although the circumstances of Elliot's acquisition of *E. dyselius* are unknown, the four black-plumaged specimens could have been gleaned from commercial lots consisting of tens of thousands of specimens (Doughty 1975). For the purpose of analysis, the holotype of *E. dyselius* may have originated anywhere in northwestern South America (see Berlioz &



Fig. 1. Holotype of Eriocnemis dyselius Elliot, 1872 (AMNH 38452).

Jouanin 1944), a region inhabited by more than 150 species of hummingbirds (Hilty & Brown 1986, Graves 1990).

I considered Salvin's hypothesis as the most likely, a priori. The possibility of hybridization was judged to be negligible because the plumage of *E. dyselius* is substantially darker and less reflective than that of any potential parental species in northwestern South America (i.e., *Coeligena prunellei, Eriocnemis nigrivestis, Heliangelus zusii, H. regalis).*

The downy tibial puffs and body proportions of *E. dyselius* clearly mark it as a member of *Eriocnemis*. I took standard measurements (rounded to the nearest 0.1 mm) of adult male and female specimens of *Eriocnemis cupreoventris, E. nigrivestis,* and *E. vestitus* (the three species most similar in size and shape to the holotype of *E. dyselius*) with digital calipers: wing chord; lengths of rectrices (from point of insertion of central rectrices); and bill length (from anterior extension of feathers) (Table 1). Color comparisons were made under nature 10× magnification (Appendix).

I used principal components analysis

	cupreoventris		ve.	vestitus	
	(n = 15)	♀♀ (n = 6)	(n = 15)	(n = 11)	dyselius ^a AMNH 38452
Wing chord	59.6-63.8	57.2-60.7	57.8-61.3	54.7-59.4	58.8
	61.6 ± 1.3	58.8 ± 1.1	59.4 ± 1.1	57.7 ± 1.4	
Bill length	16.6-18.6	17.0-19.6	15.9-18.8	17.4-19.2	17.5
	17.8 ± 0.5	18.5 ± 1.0	17.5 ± 0.8	18.5 ± 0.5	
Rectrix 1	24.5-28.2	24.6-26.6	26.2-29.7	29.7-32.8	26.9
	26.4 ± 1.1	25.8 ± 0.7	28.4 ± 1.1	31.1 ± 0.9	
Rectrix 2	26.9-31.2	26.1-28.2	28.0-31.5	31.3-35.1	29.8
	28.6 ± 1.3	27.4 ± 0.8	29.9 ± 1.1	32.9 ± 1.1	
Rectrix 3	31.9-36.6	30.7-33.3	31.1-35.3	33.5-37.7	34.6
	33.8 ± 1.5	32.1 ± 0.9	33.1 ± 1.4	35.9 ± 1.3	
Rectrix 4	36.9-42.4	34.8-38.5	35.3-39.7	35.9-41.0	37.9
	39.5 ± 1.8	37.0 ± 1.3	37.9 ± 1.5	38.9 ± 1.5	
Rectrix 5	40.4-46.3	36.0-40.1	40.6-45.3	37.6-42.2	39.5
	42.9 ± 1.7	38.6 ± 1.6	42.7 ± 1.4	39.7 ± 1.5	

Table 1.—Ranges and means (± standard deviation) of measurements (mm) of Eriocnemis cupreoventris, E. vestitus, and the type specimen of Eriocnemis dyselius Elliot, 1872.

^a All measurements on left side.

(PCA) on \log_{10} transformed measurements to reduce the dimensionality of data. Unrotated principal components were extracted from covariance matrices (Wilkinson 1989). Factor scores were projected on a bivariate plot to illustrate the relationship of rectricial measurements in *Eriocnemis* (Table 2, Fig. 2). For brevity, the holotype of *E. dyselius* will be referred to as *dyselius* in the remainder of the paper.

Results and Discussion

Currently recognized species of *Erioc*nemis (Sibley & Monroe 1990, Graves 1996) exhibit areas of glittering or brilliant plumage which probably serve as signaling badges during agonistic and sexual displays. The dull black plumage of *dyselius* lacks glittering iridescence, an observation consistent with the hypothesis of melanism. Although melanism is thought to occur at a very low frequency in the Trochilidae (e.g., Salvin 1892, Greenway 1978), the fine structure of melanism in hummingbirds has not been formally investigated, and I will only briefly address the topic here. Iridescence in hummingbirds is caused by the interference of light reflected from the upper and lower surfaces of air-filled vacuoles in melanin granules, which are closely stacked in 7-15 layers in the outer keratin of the expanded dorsal flanges of feather barbules (Dorst 1951, Greenewalt et al. 1960, Lucas & Stettenheim 1972). Perceived colors vary according to the size of the vacuoles, the thickness of melanin granules, and the an-

Table 2.—Factor loadings from a principal components analysis (PCA) of rectricial measurements of *Eriocnemis cupreoventris*, *E. vestitus*, and the holotype of *Eriocnemis dyselius* Elliot, 1872.

Variables	PCA 1	PCA 2	PCA 3
Rectrix 1 (innermost)	0.0314	-0.0054	0.0076
Rectrix 2	0.0298	-0.0035	0.0005
Rectrix 3	0.0195	0.0055	-0.0102
Rectrix 4	0.0093	0.0150	-0.0071
Rectrix 5	0.0012	0.0228	0.0090
Percent variance explained	66.2%	23.1%	8.3%

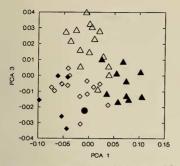


Fig. 2. Bivariate relationship of factor scores (PCA 1 & PCA 3, see Table 2) from a principal components analysis of rectricial measurements of *Eriocnemis cupreoventris* (diamonds: females = filled; males = empty), *E.* vestitus (triangles: females = filled; males = empty); and the holotype of *Eriocnemis dyselius* Elliot, 1872 (filled circle).

gle of observation. The intensity of color is enhanced by reflectance from multiple layers of granules. An overabundance and random placement of melanin granules in the keratin would lead to a disarrangement of the reflective layers, the absorption of light, and a damping of iridescent brilliance.

Eriocnemis cupreoventris and E. vestitus are remarkably similar in size and shape and melanistic specimens would be difficult to distinguish. The mean bill and wing lengths of the respective sexes of the two species differ by 0 to 3.7%. The difference in mean rectrix length varies from 0.4% to 7.5% in males and 5.1% to 20.9% in females. Comparison of raw measurements and inspection of bivariate plots of PCA variables extracted from rectricial measurements show that dyselius is most similar in size and shape to male E. cupreoventris (Table 1, Fig. 2). The bill length of dyselius (17.5 mm) falls outside the range of measurements for *E. nigrivestis* (males: n = 15; 14.4–15.8 mm, $\bar{X} = 15.1 \pm 0.5$, and females: n = 6; 15.6–16.5 mm, $\bar{X} = 16.0 \pm$ 0.3; see measurements in Graves 1996),

thus eliminating that species as a possibility.

Feather shape of *dyselius* provides additional clues as to its identity. The outermost rectrices and longest uppertail coverts of *E. cupreoventris* are slightly narrower and more attenuate than those of *E. vestitus* and *E. nigrivestis*, although some overlap occurs among the species. The shape of these feathers in *dyselius* is most similar to those of *E. cupreoventris*.

When viewed head-on under direct light, the throat of dyselius emits a dull plumbeous iridescence but exhibits no evidence of a centrally demarcated area corresponding to the gorget found in both sexes of *E. nigrivestis* and *E. vestitus. Eriocnemis cupreoventris* lacks a defined gorget. Instead, the entire throat and upper breast exhibits brilliant iridescence in both sexes. The gradation of feather size, shape, and reflectivity across the throat of dyselius resembles that of *E. cupreoventris*. Moreover, the pattern of melanization in dyselius corresponds precisely with the distribution of iridescent plumage in *E. cupreoventris*.

In summary, the holotype of Eriocnemis dyselius corresponds well in size to male E. cupreoventris. Subtleties of rectrix shape, the lack of a well-developed gorget, and the general pattern of melanization of dyselius also are consistent with Salvin's (1892) hypothesis that dyselius is a melanistic example of E. cupreoventris, and provide no reason to believe that dyselius represents either a hybrid or a valid species. Thus, the name Eriocnemis dyselius Elliot, 1872 correctly is placed in the synonymy of Eriocnemis cupreoventris (Fraser, 1840).

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Literature Cited

- Banks, R. C., & N. K. Johnson. 1961. A review of North American hybrid hummingbirds.—Condor 63:3– 28.
- Berlioz, J., & C. Jouanin. 1944. Liste de Trochilidés trouvés dans les collections commerciales de Bogota.—Oiseau 14:126–155.
- Bleiweiss, R. 1988. Plumage ontogeny and taxonomic status of the Dusky Starfrontlet *Coeligena orina* Wetmore.—Bulletin of the British Ornithologists Club 108:127–131.
- Cory, C. B. 1918. Catalogue of birds of the Americas. Part 2, No. 1.—Field Museum of Natural History Zoological Series 13:1–315.
- Dorst, J. 1951. Recherches sur la structure des plumes des Trochilidés.—Mémoires du Muséum National D'Histoire Naturelle (Série A. Zoologie) 1:125– 260.
- Doughty, R. W. 1975. Feather fashions and bird preservation: A study in nature protection. University of California Press, Berkeley, California, 184 pp.
- Elliot, D. G. 1872. Description of a supposed new species of humming bird of the genus *Eriocnemis*.— Ibis (Second Series) 2:293–295.
- Fjeldså, J., & N. Krabbe. 1990. Birds of the high Andes. Zoological Museum, University of Copenhagen, Denmark, 876 pp.
- Fraser, [L.] 1840. [Characters of several species of humming-birds, which had been placed in his hands by the Earl of Derby].—Proceedings of the Zoological Society of London (part 8):14–19.
- Graves, G. R. 1990. Systematics of the "green-throated sunangels" (Aves: Trochilidae): valid taxa or hybrids?—Proceedings of the Biological Society of Washington 103:6–25.
- ———. 1993. Relic of a lost world: a new species of sunangel (Trochilidae: *Heliangelus*) from "Bogota."—Auk 110:1–8.
- 1996. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 2. Hybrid origin of *Eriocnem*is soderstromi Butler.—Proceedings of the Biological Society of Washington 109:764–769.
- 1997a. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 3. Parentage of *Lesbia ortoni* Lawrence.—Proceedings of the Biological Society 110:314–319.
- —. 1997b. Diagnoses of hybrid hummingbirds (Aves: Trochilidae). 4. Hybrid origin of Calothorax decoratus Gould.—Proceedings of the Biological Society 110:320–325.
 - -, & R. L. Zusi. 1990. An intergeneric hybrid

hummingbird (*Heliodoxa leadbeateri* × *Heliangelus amethysticollis*) from northern Colombia.— Condor 92:754–760.

- Greenewalt, C. H., W. Brandt, & D. D. Friel. 1960. Iridescent colors of hummingbird feathers.—Journal of the American Optical Society 50:1005–1016.
- Greenway, J. C., Jr. 1978. Type specimens of birds in the American Museum of Natural History. Part 2.—Bulletin of the American Museum of Natural History 161:1–305.
- Hilty, S. L., & W. L. Brown. 1986. A guide to the birds of Colombia. Princeton University Press, Princeton, New Jersey, 836 pp.
- Hinkelmann, C., B. Nicolai, & R. W. Dickerman. 1991. Notes on a hitherto unknown specimen of Neolesbia nehrkorni (Berlepsch, 1887; Trochilidae) with a discussion of the hybrid origin of this 'species.'—Bulletin of the British Ornithologists Club 111:190–199.
- Lucas, A. M. & P. R. Stettenheim. 1972. Avian anatomy. Integument, Part 2. United States Department of Agriculture, Washington DC. Agricultural Handbook 362:341–750.
- Ortiz-Crespo, F. I. 1972. A new method to separate immature and adult hummingbirds.—Auk 89:851– 857.
- Peters, J. 1945. Check-list of birds of the world. Vol. 5. Museum of Comparative Zoology, Cambridge, Massachusetts, 306 pp.
- Salvin, O. 1892. Catalogue of the birds in the British Museum, Vol. 16. London. 703 pp.
- Sibley, C. G., & B. L. Monroe, Jr. 1990. Distribution and taxonomy of birds of the world. Yale University Press, New Haven, Connecticut, 1111 pp.
- Wilkinson, L. 1989. SYSTAT: the system for statistics. SYSTAT, Inc., Evanston, Illinois, 822 pp.

Appendix

Description of Eriocnemis dyselius Elliot, 1872. The plumage of dyselius is entirely black (with the exception of tibial plumes), glossier on the crown (bluish sheen), with faint greenish reflections on the uppertail coverts and pronounced bronzy-green reflections on the innermost secondaries. Sides of the head, lores, and auriculars, are about same color as the hindneck and crown but lack the bluish sheen. Dorsal body plumage is subtly darker than ventral plumage; feather bases are grayish-buff, palest near the rachis. The throat lacks a structurally demarcated gorget; however, the terminal discs reflect a faint plumbeous iridescence in direct light (dull black in diffuse light). The basal margins of some throat feathers are buffy-white, imparting a somewhat mottled or scaled appearance to the throat. Undertail coverts are black with a bluish sheen. Primaries are dull black but paler than the dorsal body plumage. Rectrices are glossy bluish-black on the dorsal and ventral surfaces. The well-developed tibial "puffs" are white.